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# BIOLOGICAL BULLETIN

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## CORRELATION IN THE DEVELOPMENT OF FASCIOLARIA.<sup>1</sup>

O. C. GLASER.

The following pages contain in abstract an account of the embryology of the prosobranch *Fasciolaria tulipa* (var. *distantis*), and a discussion of such occurrences in its development as seem to me to be of general interest.

### I. THE CANNIBALISM OF FASCIOLARIA EMBRYOS.

The breeding season of *Fasciolaria* at Beaufort, N. C., lasts from about the first of May until the first of July, although egg-cases containing various stages of development were occasionally found in August. The capsules, held together by a basement membrane fastened to oyster shells, conchs or wharf-piling, occur in bunches of 15-30 varying in size from one half to three inches across.

When fresh they are soft and so translucent that the pink or white eggs suspended in their albuminous contents give their color to the whole mass; later, however, the egg-cases become firm and elastic, and obscured by the algæ, polyzoöns, and other organisms which grow over them. Often isolated capsules, or bunches containing only a few are found. These are produced either by females interrupted at laying, or by young females, which usually deposit fewer and smaller capsules than the old ones. The last capsule to be laid in a bunch, whether deposited by an old or

<sup>1</sup> For the privilege of collecting the material on which this work was done I am indebted to the Hon. George M. Bowers, U. S. Commissioner of Fisheries. The preparation of this paper was begun during my tenure of the Adam T. Bruce fellowship in the Johns Hopkins University, and was finished for the press in the Zoölogical Laboratory of the University of Michigan.

young female, often lacks either the upper or lateral flanges, or both.

The number of eggs in each capsule is much greater than has been supposed, and has an important effect on development. By actual count I found that one capsule contained 2,308 eggs. The highest estimate which I remember to have seen in the literature is from 600 to 800. The ova, densely crowded with pink, brown, or white yolk spherules, which are separated from an unusually large and eccentrically placed germinal vesicle by

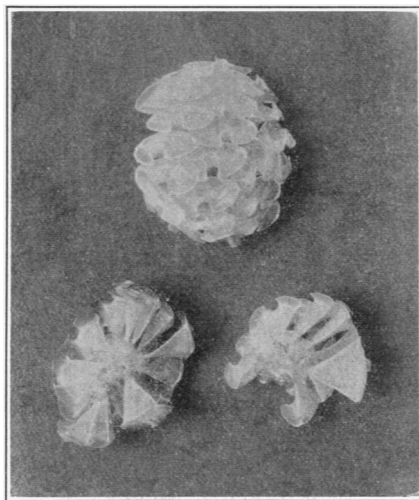


FIG. 1. Egg-cases of *Fasciolaria tulipa* (var. *distans*) one half natural size.

a zone of clear cytoplasm, vary in diameter from .17 to .25 mm. Even eggs of this size are minute enough to produce the same optical effects that much smaller spheres do, for in making a numerical estimate in a watch crystal one almost invariably supposes fewer to be present than the dish actually contains.

Of all the eggs in fresh capsules only a few are fertilized and develop. The remainder with the germinal vesicle intact are ingested, usually within a week after deposition by the developing embryos. After the eggs have been swallowed several days their germinal vesicles fragment, their pellicles disappear, and their yolk finally is digested.

The fertilized eggs are so few in number and so difficult to find

that the only method of determining the average number per capsule was by finding the average number of larvæ in the later stages. The number of fertilized eggs in each capsule cannot have been less than the number of larvæ that come from it. There are reasons moreover, such as the frequency of accidents and the occurrence of dwarfed embryos, easily overlooked, for believing that the number of fertilized eggs exceeds the number of young found in later stages. The contents of 145 advanced capsules showed 6.2 larvæ in each as an average between a maximum of 15 and a minimum of 2. Between these extremes all degrees of fertility occurred.

The stages of development found in a single capsule are as variable as the number of larvæ. Two cell stages may occur in the same case with advanced embryos. It is difficult therefore to form an idea of the rate at which an individual egg develops, particularly as development ceases shortly after the embryos are removed from the capsules. Judging from the great variety of stages found in a single egg-case one may conclude either that not all the eggs are fertilized in the oviduct, but that some are impregnated after the capsules have been deposited, or that for some reason certain ones undergo a longer resting period than others. The importance of these discrepancies at the beginning of development becomes apparent in later stages.

After the early developmental processes have been passed through a larva results so irregular that no two individuals of this age are alike. Fig. 2 omits two eggs which this larva had swallowed, but will serve very well without these to give an idea of the general external appearance of the embryo before the crisis of its larval life has occurred. The larva is represented as viewed from the ventral surface. Anteriorly is the head vesicle (*h.v.*) and posteriorly the body vesicle (*b.v.*). Between the two, under the right external kidney (*ex.k.*), two of the yolk spheres, derived from the four macromeres of the segmentation period, can be seen. The ectoderm of the body and head vesicles lacks definite cell boundaries, though the indefiniteness is much greater in the anterior than in the posterior region. Each nucleus of the ectoderm stains deeply and is surrounded by vacuoles which decrease in size inversely as their distance from it. Those

furthest away from the nucleus are the smallest, and finally only minute scattered granules can be seen where one cell abuts upon another.

The mouth (*mt h.*) is nearly perpendicular to the antero-posterior axis of the body. On each side of it are two pear-shaped patches of highly vacuolated ectoderm which I described ('04) as early stages of the external kidneys, two organs which in

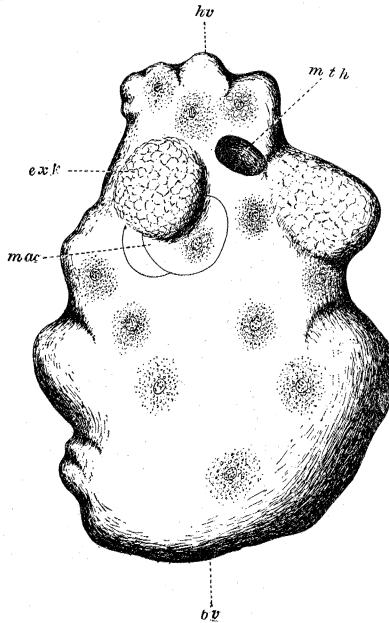


FIG. 2. Pre-cannibal larva of *Fasciolaria*; *b.v.*, body vesicle; *ex.k.*, external kidney; *h.v.*, head vesicle; *mac.*, macromere; *mt h.*, mouth. Zeiss *D obj.* 2 oc. Drawn by Mr. Carl Kellner.

*Fasciolaria* reach surprising proportions and probably take a most active part in the excretion of waste products.

The cells of the excretory organs differ from the ordinary ectoderm cells chiefly in the great size of their vacuoles and nuclei. They resemble at this stage the ordinary ectoderm in the comparative indefiniteness of their boundaries, which curiously enough are perfectly distinct at earlier as well as at later stages of development. This disappearance and subsequent reappearance of cell boundaries is due I believe to changes in

the intra-cellular pressure, which varies with the size and number of the vacuoles ('05).

When the larvæ have attained the external condition described, the process of cannibalism begins. The eggs which up to that time are quite uniformly scattered throughout the albumen of the capsules are collected in more or less dense groups by the action of the cilia around the mouths of the embryos. Some hours after the eggs have been collected in the center of each capsule smaller groups, still more densely packed, can be seen, and at the end of two or three days all have been gathered into from two to fifteen spheres which are the cannibals, stuffed almost beyond comprehension. All larvæ which secure sufficient eggs finally have the appearance of the one shown in Fig. 3.

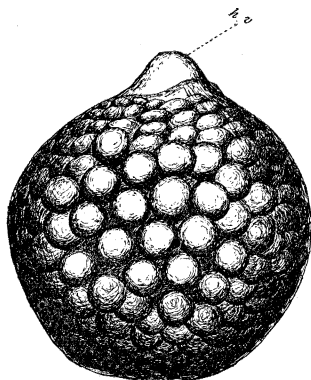


FIG. 3. Fully gorged cannibal larva of *Fasciolaria*. *h.v.*, head vesicle. Enlarged 20 diameters. Drawn by Mr. Carl Kellner.

This embryo is a fully gorged cannibal, so distended with eggs that the body wall is scarcely visible, and the mouth and excretory bodies are quite obscured by the dark background of yolk. All that can be definitely made out is the folded and slightly irregular head vesicle (*h.v.*) which marks the anterior end. Larvæ in this condition are comparatively regular, being in fact nothing more than balls of eggs held together by exceedingly thin transparent membranes. The diameters of fully gorged cannibals vary from 1.16 mm. to 1.90 mm. depending on the actual number of eggs that have been taken in. The average diameter of larvæ in this condition is about 1.48 mm. and one

near this average contained by actual count over 300 eggs. Some larvæ of larger size undoubtedly contain more eggs, and some are entirely devoid of them.

What regulates the number of eggs swallowed? As already noted, eggs in all stages of segmentation may occur in the same capsule. Similarly in older capsules larvæ of very different degrees of development may occur together. Of these the most advanced, the first to be ready to swallow, gets most of the eggs, while its tardy mess-mates must take what remains. Those that are very late in reaching the point where they can ingest eggs often get none at all. They remain dwarfed and subsist on the jelly as best they can. Most of these dwarfed larvæ degenerate or are ingested by the cannibals, but occasionally some hatch as "runts" which are normal in all respects except size.

Of the larvæ which develop at a uniform rate those which have the most distensible mouths and the most violent ciliary action in the adoral field get more eggs than those with less distensible mouths and a less active ciliary mechanism. Thus in general, the number of eggs which a given larva secures depends on how early it enters the period of cannibalism and how rapidly and easily it swallows.

Repeated experiments were tried to find out the effect of artificially increasing the food supply of a given larva. One of these experiments gave a very remarkable result.

I was not able to keep the larvæ in a healthy condition outside of the egg cases, nor to satisfactorily reseal a capsule once opened. The problem of artificially increasing the food supply of a given embryo offered some difficulties until I tried the plan of injuring some of the larvæ inside of a capsule. This can be done easily by allowing them to drift into a corner of the egg case, holding them there by pressure on the rest of the capsule and then compressing them with a pair of strong forceps. With care one or two larvæ can be kept out of the corner, and all those which have been coralled can be injured in the manner described.

An injury to the excessively thin body-wall has the same effect as a hole in a bag of grain. The eggs which have been swallowed roll out and leave an empty membrane behind. In this way a thousand eggs, which have been swallowed once, may be

set free. In the experiments which I made all but two or three larvæ in each of a large number of capsules were forcibly injured, and their undigested contents offered to the uninjured larvæ. These, although fully distended, in every case began to devour the additional eggs offered them, and in three or four days had mastered twice as many as had before fallen to their respective lots. One experiment, which was particularly successful, consisted in an attempt on my part to ascertain whether one larva would eat all the eggs which had been taken in by its competitors. This was accomplished by first injuring two of these and waiting until the extra number of eggs had been disposed of. Then two of the remaining larvæ were injured and the eggs which they contained — some of which had been swallowed once and others twice — were offered to the three uninjured inhabitants of the capsule. After this second offering of eggs was disposed of, two of the remaining three larvæ, which had grown to more than double their original size, were injured, and their contents offered to the sole survivor. This individual, already excessively gorged, began to ingest the eggs which had been swallowed from one to three times; unfortunately the elasticity of its body was not equal to the undertaking and the larva burst from over-eating before it had finished.

Over-feeding comparable to what happened in these experiments may take place without human interference. It is easy to see how the natural disturbances to which the capsules are subject might be sufficiently violent to burst some of the larvæ whose contents then would be devoured by the survivors. I am convinced that this actually takes place, since the larvae in those capsules which contain only two or three are always much larger than the average. From these observations and experiments I believe that the number of eggs secured depends on promptness and structural aptitude for seizing and swallowing.

## II. THE EXTERNAL AND THE ACCESSORY EXTERNAL KIDNEYS OF FASCIOLARIA.

*Development.*—The external kidneys, also known as “excretory cells” (Conklin) or “subvelar masses” (Osborne) and very generally called “*Urnieren*” by German writers, originate early



in *Fasciolaria*, and are remarkable not for their size and position on the embryo, but also because they seem to take a very important part in the economy of the larva. Both the presence and the activity of these remarkable bodies are of interest when considered in the light of the feeding habits just described, for these, as might be expected, tax to the utmost the powers of assimilation and excretion.

Without considering the cytological changes which occur in the kidney cells, and which have been described fully in another place ('05) I will mention some of the more important alterations which involve the entire organs. What Conklin ('97) has said of the excretory cells of *Crepidula* applies equally well to those of *Fasciolaria*: "In the early stages these cells form a part of the

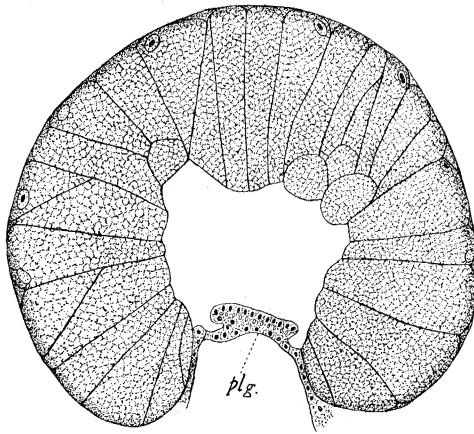


FIG. 4. Vertical section through external kidney of *Fasciolaria* showing connection with unmodified ectoderm and the plug (plg.) of undifferentiated cells which later fill the lumen. *Leitz 3 obj. 8 oc.*  
2. Drawn by Mr. Carl Kellner.

ectodermic layer, but as the embryo grows older they grow more prominent, and the whole mass is constricted at the base, so that it becomes pear-shaped, the narrow end being attached to the embryo, and the larger end being distal. The surrounding ectoderm cells crowd in at the neck of this constriction and work their way entirely beneath these excretory cells."

In *Fasciolaria* three very important changes take place in addition to those already mentioned. The ectoderm cells which

“crowd in at the neck of the constriction” do more than this, for some of them coming from opposite sides join to form a plug which projects into the hollow of the rounded excretory organ. (Fig. 4, *plg.*) As the excretory organs at later stages have no lumens whatever, I conclude that these cells become modified secondarily into excretory cells like the primary ones.

The second important change which takes place in the external kidneys involves their position and results in the adoption of that curious relation with the velum which led Osborn ('85) to speak

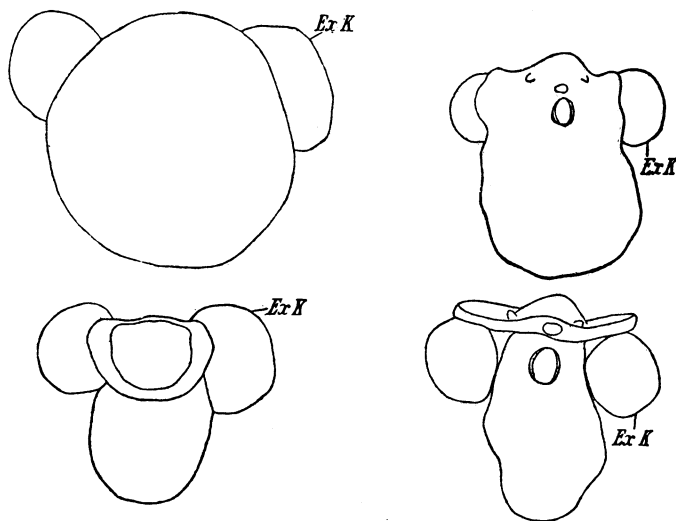


FIG. 5. Four stages in the migration of the external kidneys (*ex.k.*) from the lateral surface of the cannibal to their final subvelar position on the veliger.

of them as “subvelar masses.” When this change begins the embryo as a whole has enlarged greatly (Fig. 5), and has both by growth and by the stretching, due to the ingestion of eggs, become much wider than it was, especially at the base of the head vesicle. This increase in size brings about the removal of the external kidneys from the anterior surface of the larva to the lateral surfaces. Later the great activity in the velar ridge, by which this becomes prominent, as well as the growth of the whole anterior end of the larva, result in lifting the external kidneys upward and carrying them laterally away from the central mass of yolk on which at first they lie directly. Further lateral growth

of the velum carries the external kidneys outward and still farther away from the embryo, until finally they are far off at the sides of the body and hang down from the under side of the velum (Fig. 5). In this position the organs, which are white, viscid masses of ovate shape, having at the height of functional activity an average width of .7 mm., a length of 1.0 mm., and a depth of .9 mm., remain throughout the life of the veliger until this begins to assume the adult form. When that stage is reached the external kidneys begin to decrease in size, to degenerate, and the nuclei of the cells to disappear. Finally, in most cases, the kidneys are dropped off before the velum is resorbed. There are exceptions to this however, for often a much more intimate

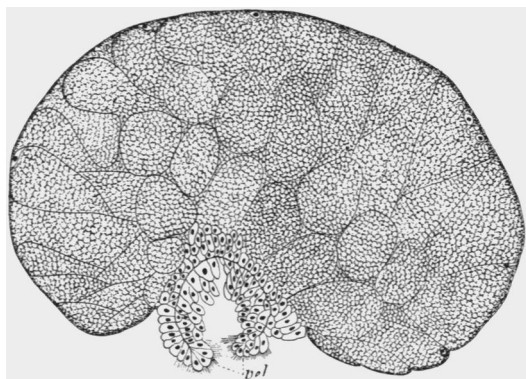


FIG. 6. Vertical section through external kidney showing the intimate relation which it may have with the velum (*vel.*). Leitz  $\frac{3 \text{ obj. } 3 \text{ oc.}}{2}$ .

relation exists between the velum and the excretory organs hanging down from its under surface. This greater intimacy is well illustrated by Fig. 6, which is a typical section of these cases. In this organ, after the original lumen had been filled by the plug cells, the fully developed velum itself grew into the small pit which remained at the proximal (final anterior) end of the kidney. In this instance the velum was so crowded in the remaining hollow of the external kidney that the velar cavity itself was entirely obliterated by the close approximation of its upper and lower walls. In cases of this kind the velum drops off with the external kidney when the veliger assumes the adult form.

This intimate connection between the velum and the kidneys recalls the "ansæ" of *Bithynia tentaculata*, described by Sarasin ('83). In this form the relation between the external kidneys and the velum is still more intimate than in these exceptional cases in *Fasciolaria*. Indeed the velum of *Bithynia* seems to be modified into a functional excretory apparatus, without having renounced its original duties as an organ of locomotion.

*Accessory External Kidneys.*—One of the most unexpected

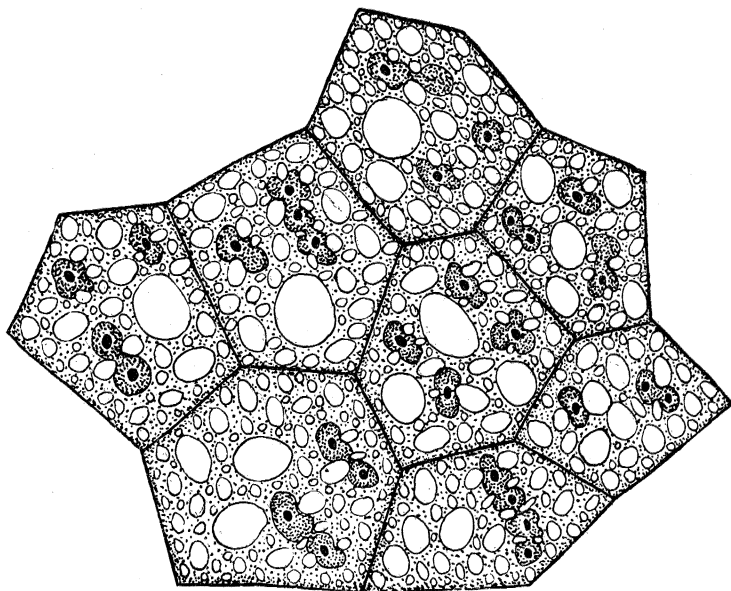


FIG. 7. Surface view of a portion of a functionally active external kidney, showing the thickened cell boundaries, the vacuolated cell contents, the amitotically dividing nuclei, and the nucleoli with their surrounding clear areas. Zeiss A obj. 4 oc.

facts which I have encountered in my study of *Fasciolaria* embryos is that in addition to the large excretory organs no small proportion of larvæ possesses, sometimes in surprising places, accessory multicellular or unicellular external kidneys. In many cases these are found on the underside of the velum just behind the great kidneys; here they may become a third as large as the primary organs. In other instances single cells of the postoral or preoral velar row, and even of the head vesicle become modified into secondary unicellular kidneys. In some

of these accessory organs amitosis was observed, and in all the same extra-nuclear signs of activity which characterize the cells of the primary kidneys.

*Function.* — Between the two extremes of development which I have described the nuclei of the external kidneys divide amitotically and the cells become polynucleated. The nuclei are large, granular, very irregular in outline, and each one has at least one nucleolus surrounded by a clear area. In addition the cells are characterized by their thick boundaries and the highly vacuolated condition of their contents.

On a former occasion ('04) I showed how the vacuoles in the cells might be traced to the halos surrounding the nucleoli, but the figures intended to illustrate this are unsatisfactory since certain features which I hoped would not appear so unnaturally prominent when reduced to one half are over emphasized. More satisfactory figures will be found in my later paper ('05). The vacuoles which in some cases can be traced directly to the extra-nucleolar halo, in others to the nucleus from which I have seen them escaping, certainly suggest a high state of metabolic activity.

In the summer of 1903, with a view to determining the nature of the activities in the external kidneys, I removed several hundred, extracted them in chloroform water and asked my father to make a careful analysis of the extract. The details of this analysis have already been published ('05) but as all the decimal points were omitted by a careless printer, I republish the following corrected summary. One liter of the aqueous extract of the external kidneys contained

N as albumen,	.1242
N as free ammonia,	.0099
N as urea or homologues,	<u>.2163</u>
Total N,	.3504

My interpretation of the above analysis was that the external kidneys excreted waste products, but a reconsideration of the evidence, shows that it can become decisive only after corresponding analyses of extracts of other tissues have been made. Regardless of the value of the chemical evidence, which is certainly not negative, I still think that all the morphological results point to the probability that the external kidneys are excretory organs.

With the aid of such evidence as I have been able to obtain, and Osborn's interesting discovery ('04) of amitosis in the endoderm, I think I may formulate a scheme to account for the transfer of materials which probably takes place. Osborn ('04) announced that he had discovered amitosis in the endoderm of the gastrulæ of *Fasciolaria* and associated, very justly, I think, these nuclear phenomena with digestion. I have been able to verify these results, not, however, until I had been thoroughly led astray by the assertion that the nuclear divisions in question occur in the gastrula stage. All my earlier larvæ show no signs either of the "cuboidal endoderm" or of the amitoses of which Osborn speaks. The latter phenomenon I finally discovered in a larva that had a velum, and was therefore well past the period of cannibalism. Fig. 8 is compounded from several sections ob-

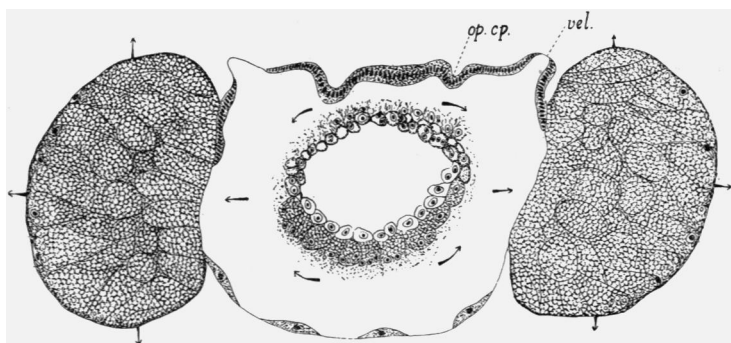


FIG. 8. Composite figure made up from several adjacent sections oblique to the antero-posterior axis. The external kidneys, not yet subvelar in position, are cut horizontally. *Op. cp.*, optic cup. *vel.*, velum. The arrows are intended to indicate the probable paths of waste products reaching the exterior from the digestive tract seen in transverse section, via the external kidneys. Leitz  $\frac{3 \text{ obj. } 3 \text{ oc.}}{2}$ .

lique to the antero-posterior axis of this larva. The œsophagus is cut transversely and the cells which compose it are dorsally, large, polynucleated, and highly granular, with vacuoles at their distal ends. The nuclei appear to have arisen amitotically. Some of these cells have burst and their contents may be seen oozing out. They bear a striking resemblance to the cells of the external kidneys.

The cells of the lateral and ventral walls of the œsophagus have a very different appearance. These, instead of being long

and granular, are very irregular in shape, the cytoplasm being almost invisible, in irregular strands, or crowded closely against the cell boundaries. In the center some of the cells have a large clear space in which the nucleus lies. The nucleoli sometimes occur in the clear vacuoles which are scattered about in the nuclei. Many of the latter are in process of amitotic division.

Around the outer margin of the lateral and ventral walls of the oesophagus many of its bounding cells seem to have broken down, whereas others are clearly engaged in this process. By this means the outline is made extremely irregular, being frayed, and fringed with granules and the fragments of cells. This breaking down of the cells, their general vacuolated appearance, the occurrence of amitosis, and the finely divided state of the chromatin in the nuclei, all indicate that these cells are actively engaged in metabolism, and the simplest supposition is that they are engaged, as Osborn has suggested, in the process of digestion.

That something is leaving these cells is demonstrated by their appearance. I believe therefore that in the course of their activity as digestive cells, they excrete waste products, and that these pass across the "body cavity" into the cavity of the velum, transude through its basal membrane into the external kidneys and through these ultimately to the exterior. The arrows are intended to give a graphic representation of this process.

*Homologies.*—The earlier writers who considered the functions of the external kidneys of gastropods fall into two general groups, those who affirm and those who deny that these organs are renal organs. The same writers however have been at much greater discord with regard to the homologies. Thus Salensky ('72) homologized the external kidneys of *Calpytrea sinensis* with the primitive kidneys of pulmonates. Fol ('75) did the exact reverse by attempting to homologize the "Urnieren" of pulmonates with the primitive kidneys of prosobranchs. Bobretsky ('77) who describes the "Urnieren" of *Nassa mutabilis*, *Natica*, and *Fusus*, seems to have accepted the homologies advocated by Salensky. Bütschli ('77) in the same year, however, in a paper on *Paludina vivipara* took strong exception to Fol's homology. He pointed out that this supposed homology was between totally different structures, and that while the primitive kidneys of *Paludina*

might be homologous with the primitive kidneys of *Lymnæus* and *Planorbis*, the external excretory organs "Urnierenzellen" of these forms could not be homologized with the primitive kidneys of *Paludina*.

Thus the significant fact was brought out that there are two kinds of "Urnieren," the one, since proved to be of mesodermal origin (*Paludina*, *Planorbis*), opening to the exterior by a pore, the others, collections of modified ectoderm cells, situated either on the postoral row of the velum (*Lymnæus*, *Planorbis*), or behind the velum (*Crepidula*, *Fulgur*). The confusion due to the attempts to homologize the external kidneys of prosobranchs with the primitive kidneys of pulmonates, and the converse proposition of tracing an homology between the external kidneys of pulmonates and the primitive or head kidneys of prosobranchs, was probably greatly increased because all these structures were called by some German writers "Urnieren." In this connection it is interesting that Korschelt and Heider ('93) in copying Bobretsky's figures for their text-book changed the labelling so that "Un" is replaced by "Ex."

Rabl ('79) came to the conclusion that the external kidneys of *Planorbis* were a part of the velum, and that they have nothing to do with the "head kidneys." Sarasin ('82) describes a most intimate connection between the velum and the external kidneys in *Bithynia tentaculata*. In fact he described the two under one name, the "Ansæ." In speaking of their homologies he says: "Nach den Erfahrungen von Bobretsky, Bütschli und mir, liegt auf jeder seite der Prosobranchier Embryonen, ein Häufchen grosser Ectodermzellen, das bei *Paludina* und *Bithynia* mit Wimperöffnung nach aussen mündet. Nach Bütschli und Fol finden sich diesselben bei *Planorbis*. Ist dies richtig, so haben die Süsswasser Pulmonaten zwei Organ paare, die als Urniere zu deuten sind ein vorderes und ein hinteres Paar. Hat Rabl recht dass die von Bütschli zuerst gefunden grossen Zellen bei *Planorbis* und *Lymnæus* zum Velum gehören, so sind wahrscheinlich die von Bütschli und mir bei *Paludina* und *Bithynia* gefundenen Organe den hinternen Urnieren der Süsswasser Pulmonaten homolog." Sarasin's position, except that it admits the ectodermal origin of the primitive kidneys in *Paludina*, is in the present state of our knowl-



edge tenable. Erlanger ('92), though denying the excretory function of the "Ansæ" of *Bithynia*, conceded that on morphological grounds these cells might be considered the equivalents of the peculiar velar cells of the pulmonates and of the marine prosobranchs.

Heymons ('93) introduced another source of confusion by attempting to homologize the excretory cells of opisthobranchs with the external kidneys of prosobranchs. This homology seems far-fetched, since the excretory cells of *Umbrella* are situated near the anus of the larva, though they originate much further forward. This difference in position seemed of no importance to Heymons, since, as he says, McMurrich had already shown that the excretory cells may lie at various distances behind the velum. Conklin ('97) says in reply: "this difference in position seems to me, however, to be a very considerable one. In all prosobranchs these cells lie close behind the velum, while in *Umbrella* they are removed from that structure by almost the whole diameter of the embryo. Further, the fact that they sink into the interior in *Umbrella* would indicate that they are different from the excretory cells of prosobranchs."

Conklin ('97) finds that the "external excretory cells" of *Crepidula* have no connection with the velum. This is also true, in a sense, of *Fasciolaria*. In this form the external kidneys originate long before the velum, so that their ultimate connection with that organ is not primitive but secondary, and due to their origin near the place where the velum originates. In this respect they are not fundamentally a part of the velum, any more than the external kidneys of *Crepidula*.

It is obvious from the literature considered so far that the discussion of homologies has involved at least three different kinds of excretory organs. In order to emphasize the differences I shall henceforth call those mesodermal, or possibly ectodermal, structures of pulmonates and prosobranchs which open to the exterior through a pore, primitive kidneys; those modified ectodermal excretory cells which may occur in addition to primitive kidneys, external kidneys; and finally such external organs as Heymons and others have described in opisthobranchs, excretory cells.

Anyone who has seen Stauffacher's ('98) beautiful figures of the primitive kidney of the trochophore of *Cyclas cornea* can never compare similar structures with external kidneys in prosobranchs and pulmonates, or excretory cells in opisthobranchs. Meisenheimer ('98) introduced a complication however, for his very complete study of the development of *Limax maximus* leaves almost no doubt that the primitive kidney of this gastropod is of purely ectodermal origin. The reasons which Stauffacher has advanced that the primitive kidney of *Cyclas* is mesodermal, are as convincing as Meisenheimer's that in *Limax* it is ectodermal, so that it is necessary for the present to subdivide the group of primitive kidneys into ectodermal primitive kidneys and mesodermal primitive kidneys. If the conclusions of Stauffacher and Meisenheimer be indeed correct, then two sets of homologies can be granted; the mesodermal primitive kidneys of prosobranchs, pulmonates and lamellibranchs may be homologous; and the ectodermal primitive kidneys in the same groups may be homologous. No homology however can be granted between a primitive kidney of mesodermal and one of ectodermal origin without doing violence to the whole conception of homologies. Whether a conception which separates organs as much alike in structure and probably in function as the ectodermal and mesodermal primitive kidneys of larval molluscs should be violated, is a question which at present I do not feel able to discuss.

Are the external kidneys homologous with ectodermal primitive kidneys? I believe that there is no more reason to homologize external kidneys with ectodermal primitive than with mesodermal primitive kidneys, for the differences between external kidneys and primitive kidneys, of whatever layer, are the same. That in the one case both organs should originate from the same germ layer is no criterion on which to base homologies, for if it were we should be logically driven to homologize not only all ectodermal structures, but all structures of whatever origin.

In considering the relations of the larval excretory systems of molluscs it seems to me to be of great importance to keep the differences which I have tried to emphasize constantly in mind, but the distinctions once made, the task of recognizing true homologies is by no means a simple one. Possibly all meso-

dermal primitive kidneys are homologous, and possibly all ectodermal primitive kidneys are, but certainly not all external kidneys. The occurrence of unicellular or multicellular accessory external kidneys in different regions of embryos already so well endowed with excretory organs as *Fasciolaria* shows that the embryological measuring rod which has been so carefully applied to these larval structures of molluscs is less accurate than some of the investigators who have used it for the discovery of alleged detailed relationships.

### III. THE ORIGIN OF THE HABIT OF CANNIBALISM.

Even though there are differences in the early extra-ovarian histories of the food products, the consumption of eggs and embryos by the developing larvæ of *Fasciolaria* is fundamentally similar to those other cases among gastropods in which certain young are used as food after being broken down, or are preyed upon directly by their competitors. It seems to me justifiable, therefore, to include all these methods of nutrition, based on the consumption of materials derived from the ovary of the mother, but not contained within the eggs from which the consumers come, under one term, cannibalism. The various degrees to which cannibalism is developed in different gastropods have been arranged in series by earlier writers, and though this series is both interesting and instructive it has no phylogenetic significance, and I shall try to show that the phenomenon in *Fasciolaria* can be explained independently.

McMurrich ('85) noticed that some of the "ova" in the capsules of *Crepidula fornicata*, *C. plana* and *C. convexa* break down and are used as food by the survivors, although this process is not so pronounced as in *Purpura floridana*. Koren and Danielssen ('57) described the case of *Buccinum undatum* which is very similar to that of *Fasciolaria* in the disproportion between the number of embryos developing in the capsules and the number of eggs furnished by the female. *Buccinum*, however, differs from *Fasciolaria* because many of the ova, which do not form embryos, divide. Carpenter in the same year ('57) corrected the view of Koren and Danielssen that the embryos originate by conglomeration, by describing the development of *Purpura lapillus* in

which from 12 to 30 eggs develop into embryos, whereas each of the remaining 500 or 600 divides without regularity into from 14 to 20 fragments.

Selenka ('72), who confirmed Carpenter's results, did not consider the division of the "sterile" eggs equivalent to the regular segmentation of the fertile ones, not only because of the irregularity of the former process, both as to form and occurrence, but also because he found no nucleus. *Neritina fluviatilis*, according to Blochmann ('81), has capsules in which all the eggs are provided with nuclei that take the usual part of the formation of polar bodies and female pro-nuclei. After these processes no regularity can be detected in the divisions of the sterile ova, the later behavior of which led Blochmann to agree with Bütschli ('77) that these eggs are unfertilized.

Brooks ('77) observed that of the 6 to 20 eggs in the capsules of *Urosalpinx cinerea*, all undergo development normally, though exceptionally some may break down and serve as food for the survivors. This case of exceptional cannibalism furnished McMurrich (*loc. cit.*, p. 408) with "a clue to the manner in which the phenomena seen in *Fasciolaria*, *Purpura lapillus*, etc., have been brought about. An occasional egg in a capsule has from some cause or other broken down, and has been drawn into the digestive cavity of the developing embryos. This process having proved useful is continued, and an arrangement such as I have described above for *Purpura floridana* obtained. From this it is but a step to what occurs in *Buccinum*, *Purpura lapillus* and *Neritina*. In *Fasciolaria* the process is, as far as we know at present, at its culmination."

This series was not conceived of as genetic, for this would have been justified only if it had been previously shown that each of the forms mentioned was evolved from one next lower in the scale of cannibalism. That such has been the history of cannibalistic prosobranchs is not supported by any evidence known to me, and the series is therefore probably a collection of graded parallelisms.

The real clue seems to me to lie in another factor which, as McMurrich himself pointed out, is invariably present where cannibalism has advanced to any great extent. "This is (*loc. cit.*,

p. 409) the non-fertilization of the majority of the ova, whereby it is impossible for them to develop to any great extent, and whereby they naturally break down when they have endeavored to segment. We see this in *Neritina*, *Buccinum* and *Purpura lapillus*. In *Fasciolaria*, as stated above, the process reaches its climax, and in this case the sterile, nutritive ova do not show the least trace of segmentation, nor do they ever show signs of maturation."

This second factor seems to me most important, and in view of recent results on the development of the germ cells of gastropods, places the origin of cannibalism in a new light. In the first place the ingested materials may consist of undivided eggs, or of embryos or of a combination of these classes of constituents. Thus in *Neritina* and *Fasciolaria* the ingested eggs do not divide. In *Buccinum* most of the ingested ova divide, though some do not, and in *Crepidula*, *Purpura* and *Urosalpinx*, the ingested materials are derivatives of either early or late stages of development. The habit of *Fasciolaria*, though coming in the class with that of *Neritina*, also resembles that of *Crepidula*, *Purpura* and *Urosalpinx*, for the abnormal larvæ of the pre-cannibal period, as well as many of the abnormal late ones, including some dwarf larvæ, are ingested together with the unfertilized eggs. That these materials are taken in by the embryos requires no explanation in this connection, for not only are they obviously useful as food, but the structures in virtue of which the larvæ cannot help ingesting all the available substances in their environment were evolved, for locomotion and for swallowing other things, in all probability long before *Fasciolaria* exchanged its pelagic larval life for the safer one within capsules. To explain the origin of the habit of cannibalism it seems to me necessary to answer only two questions: (1) Why do some of the embryos break down? (2) Why are many of the eggs infertile? By answering these questions materials to be swallowed are accounted for: the consumers, and the mechanism by which the consumption is brought about, are the results of that portion of the phylogenetic history of *Fasciolaria* which preceded the origin of cannibalism. Given therefore ingestors, and materials to ingest, cannibalism follows as a natural consequence, needing no further explanation.

That some of the embryos break down is due, in *Fasciolaria* at least, to the fact that they have been outstripped in development by their competitors, whose superior strength, traceable to individual differences in the sizes of the fertile eggs, in the time and places of fertilization, in the ability at various stages to withstand the effects of exposure at low tide, or the jostling and even injuries to which the capsules are naturally exposed, probably enables these more fortunate ones to set up such lively currents by means of their cilia that their weak relatives are either whirled about until seriously harmed, or are so crowded into the mass of collected food ova that injury is certain and death probable. I do not believe that it is necessary, therefore, to trace the sterile eggs historically to degenerating embryos, for even if it were easy to see how selection could occur in this particular case, the physical conditions which account for the breaking down of some of the embryos at the present time, were probably always operative and seem to me of themselves to explain the facts sufficiently well.

That many of the eggs are unfertilized is more difficult to understand. This is true of *Fasciolaria*, of *Neritina* (Bütschli, Blochmann), and of *Purpura* (Selenka). In this last form Selenka was not able to discover a nucleus. The infertile eggs of *Fasciolaria* do not react to the influence of chemicals, though in some cases when a few drops of ammonia were added to the water Professor Conklin found that a number of eggs formed protrusions at one end. I have repeatedly tried artificial fertilization, with perfectly fresh eggs, in pure sea water, in a mixture of sea water and the albuminous contents of the capsules, or in the pure albumen. In no case did I succeed in finding more than the usual number of segmenting eggs in such collections, and in no case did the undivided ones seem to have attracted the spermatozoa. Since fertilization normally precedes maturation in the gastropod ovum, I conclude that these eggs are imperfect.

In what does their imperfection consist? This is a question which I cannot answer. It seems to me, however, that the dimorphism of the spermatozoa may point the way to a solution.

Meves ('02) described most remarkable differences between the development of the oligopyrene or worm-shaped spermatozoa and the eupyrene or ordinary hair-shaped spermatozoa of

*Paludina*. These differences in development first become manifest by the occurrence of two sizes of primary spermatocytes, the larger of which give rise to the oligopyrene spermatozoa, whereas the smaller ones give rise to the eupyrene forms. When the larger primary spermatocytes undergo maturation no reduction takes place, but the normal number of chromosomes (fourteen for *Paludina*) appears at the nuclear plate. These chromosomes are so distributed in the ensuing division that one of the resulting daughter cells (secondary spermatocytes) has four and the other has ten. When the secondary spermatocytes divide to form the spermatids, only one of the chromosomes of the secondary spermatocytes undergoes division, all the others (three for one class of spermatocytes and nine for the other class) degenerate. In this way it happens that the nucleus of the oligopyrene spermatozoa is composed of a single chromosome, whereas that of the functional eupyrene sperms has seven.

*Fasciolaria*, in company with a large number of other proso-branches, has two kinds of spermatozoa, and there can be little doubt that these correspond respectively to the oligopyrene and the eupyrene sperms of *Paludina*. What the reason for this dimorphism may be is not clear, but so far as I can see, there is no evidence to show why it might not also occur among eggs, particularly of a form presenting such well marked differentiation of its male sexual elements as *Fasciolaria* does.

That *Fasciolaria* has two kinds of primary oöcytes which differ most remarkably in their reactions with spermatozoa, and consequently in their ultimate fate, is beyond dispute. This difference may possibly be due to an homology between the infertile oöcytes and those primary spermatocytes which give rise in the manner described by Meves to the oligopyrene spermatozoa. Whether further investigations establish this homology or not, the presence of the infertile eggs is the keystone of the conditions that determine cannibalism. The origin of this process therefore is to be sought in those circumstances that determine the formation of the sterile ova. That these ova should be ingested follows from the automatism of the larvæ, based on structures much older than the habit of cannibalism, and not to be explained by it. The persistence of those processes which give rise to the nutritive ova

however can be explained by the theory of selection, since this method of feeding the young is useful to the species.

The sterile ova — to whatever cause due — have an important influence on development ; indeed, all the facts which I have discussed or mentioned in the preceding pages can be united into a system of correlations, each part of which has antecedents or consequents, or both, traceable to the nutritive ova as the first link in a long chain of events. It is clear that without the sterile eggs cannibalism could not occur. It is equally clear that the larvæ prepare for this process, and that they are profoundly modified as the result of it. Thus, to consider first external characters, the frothy, irregular ectoderm of the precannibal period is well fitted for the stretching caused by the ingestion of the eggs, for these produce a distension so great that unless provision were made for it in advance a far larger number of embryos would be destroyed by it than as a matter of fact succumb.

The immediate results of the ingestion of the eggs are an entire change in the shape of the embryo, and a great increase not only in its size, but also in the size and organs of the young. The external kidneys are most clearly correlated with the cannibalism. In this case also we meet with provision, for the excretory organs appear, and are more highly developed than in any other gastropod embryo known to me, long before their chief need can be felt, and long before they have reached the highest development which they ultimately attain. The early appearance of the external kidneys, which a comparison with other prosobranchs shows to be secondary, brings about a change in their position, for if they developed at the time the velum appears, as they do in *Fulgur* (McMurrich), or after this appears as they do in *Crepidula* (Conklin), they would not be carried outwards by this organ, ultimately to hang down from its underside. The early development of the external kidneys is thus a case of cœnogenesis, and their final location on the embryo an excellent example of a conspicuous result due to a remote influence, for although this ultimate position and activity are connected with the egg-swallowing habit, this connection is indirect, since fully-developed external kidneys occur in dwarfed larvæ devoid of



ingested ova. It might be urged from this that there is not even an indirect connection between the cannibalistic habit and the excretory organs, but this is by no means true. It is an accident in the lives of the dwarfed embryos that they fail to secure any eggs, for they prepare for them as much as their more successful competitors do. The fact that the preparations for an event which never comes to pass are elaborate cannot show that this event had no influence on the lives of the anticipators. What it does show is that this influence is not direct, for the habit of preparing for cannibalism has become fixed through selection.

Another correlation of importance is the amitosis in the external kidneys and in the œsophageal endoderm. Here the need for the rapid digestion of great quantities of food material and the excretion of waste products has called forth a process unusual in embryonic cells, but, as I shall try to show in another paper, not pathological. There can be little doubt that through these amitoses other correlative changes are brought about, particularly in the development of the œsophagus, where the gaps made by the degenerating embryonic digestive cells are certainly repaired before the adult stage has been reached. Thus the whole development, from early stages to late, the structure, shape and size of the larvæ and the size and hardiness of the young, and whatever these stand for in their further lives, are affected by cannibalism, the origin of which is traceable, I believe, not to the advantage which accounts for its persistence, but to some as yet unknown cause which determines the existence of the sterile nutritive ova.

ZOOLOGICAL LABORATORY, UNIVERSITY OF MICHIGAN,  
ANN ARBOR, January 4, 1906.

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